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**EFFECT OF LEAF SHAPE ON FOREST LITTER SPIDERS:
COMMUNITY ORGANIZATION AND
MICROHABITAT SELECTION OF IMMATURE
ENOPLOGNATHA OVATA (CLERCK) (THERIDIIDAE)**

Bruce G. Stevenson and Daniel L. Dindal

Soil Ecology, State University of New York
College of Environmental Science and Forestry
Syracuse, New York 13210

ABSTRACT

Effects of leaf shape and other habitat structure variables on spider community organization and on microhabitat selection of immature *Enoplognatha ovata* in deciduous forest litter were studied in central New York. Three litter boxes of each of four litter treatments (curled maple leaves, flat maple leaves, curled filter paper disks, and flat filter paper disks) were sampled monthly from November 1979 to August 1980. Twelve similarly-sized samples of natural litter also were collected, and all litter boxes and natural litter samples were placed in Tullgren funnels for extraction of spiders.

Spider species richness was significantly greater in curled litter than in flat litter. Significant differences in the composition of hunting spider families also were found. Differences in species richness and composition of hunting spiders was attributed to differences in habitat space, according to leaf shape. Each litter treatment supported approximately the same proportion of hunting and web-building spiders and similar composition of web-building spider families. These data indicated similarity in prey resources among the litter treatments.

A three-way ANOVA for *E. ovata* density revealed significant treatment effects for leaf type, leaf shape, and month, and a significant interaction occurred between leaf type and month. More spiders were found in maple leaves than in filter paper disks and greater density occurred in curled litter than in flat litter. Preference of maple leaves and curled litter by this species may be due to increased amounts of habitat space in these microhabitats. Development of immature *E. ovata*, associated with increases in body size and greater needs for space, resulted in differential seasonal microhabitat selection. In spring and summer, spiders grew in size and litter populations (both litter boxes and natural litter) decreased. At this time mature adults were found beneath tree leaves in the forest understory layer.

INTRODUCTION

For two decades, ecologists have been concerned with the relationship between habitat structure and faunal community organization (e.g., MacArthur and MacArthur 1961). In a study of deciduous forest litter, Uetz (1974) used interstitial space between leaves as a measure of habitat space; curled or bent leaves produce greater interstitial space than do flat leaves. Litter depth and habitat space increase as the proportion of curled or bent leaves increases (Uetz 1974, Bell and Sipp 1975).

There is considerable evidence which suggests that habitat structure influences community organization of spiders inhabiting deciduous forest litter. Within a guild of wandering spiders, species richness, diversity and equitability all were correlated with litter depth and habitat space (Uetz 1975). Increased microhabitat diversity tended to increase species richness of litter spiders since a greater variety of structural microhabitats were available to them. Jocque (1973) also found that spider species diversity increased with increased depth and complexity of litter. In addition, population density of litter spiders has been correlated with litter abundance and depth (Lowrie 1942, 1948, Berry 1967, Hagstrum 1970).

Studies in which one or more of the variables of litter habitat structure are manipulated should give better understanding of the factors regulating spider species diversity within forest litter (Uetz 1975). For example, gradients of litter depth and associated habitat complexity have been studied under natural (Uetz 1976) and experimentally-modified (Uetz 1979) conditions. In both cases, wandering spider species richness increased with greater depth and complexity of litter.

The relationship between species diversity and habitat structure depends, in part, on microhabitat selection of individual species. Differential selection of microhabitats with different physical structures by potentially competing species may permit coexistence of those species (Enders 1974, Greenquist and Rovner 1976). Within forest litter, abundance of Lycosidae is greatest in shallow litter made up of flat leaves, and decreases with increasingly deep litter, containing more bent and curled leaves. Abundance of Clubionidae, Gnaphosidae and Thomisidae increases as litter becomes deeper and more complex (Uetz 1976, 1979). Spiders in the latter two families use curled leaves for retreats (Kaston 1948, 1978). There are few analyses of the use of curled leaves by web-building spiders in forest litter or other habitats, although many species build silken retreats or egg sacs in curled leaves (Kaston 1978, Lubin 1978). Spiders inhabiting *Mahonia aquifolium* Nutt. largely occupied curled leaflets (Waldorf 1976). Curled and closely parallel leaflets provided more shelter than flat leaflets.

This paper reports on the effect of altered leaf shape on community organization of forest litter spiders and on microhabitat selection of *Enoplognatha ovata* (Clerck) (= *Theridion redimitum* [L.]) (Theridiidae). The objective of this study were: (1) to test the hypotheses: (a) species richness of litter-inhabiting spiders is greater in curled litter than it is in flat litter and (b) curled litter contains more spider guilds than flat litter, and (2) to determine: (a) if leaf shape influences microhabitat selection by immature *E. ovata* and (b) if its life history affects the choice of microhabitats.

METHODS

The study was conducted at the Soil Invertebrate Ecology Laboratory at the Lafayette Experimental Station of the SUNY College of Environmental Science and Forestry in Syracuse, New York. A field experiment was conducted in a mixed hardwood stand. Dominant vegetation consisted of red oak (*Quercus ruba* L.) and sugar maple (*Acer saccharum* L.). Understory vegetation was composed of red oak, sugar maple, and black cherry (*Prunus serotina* Ehrh.). Two soil types present on this site were Cazenovia sandy loam and Ontario sandy loam (alfisols, glossoboric hapludalfs [USDA 1972]). Mull humus characterized the organic subhorizons; forest litter disappeared in about one year primarily due to earthworm activity (Pritchard 1941, Stevenson pers. obs.).

Table 1.—List of identified species extracted from litter boxes and the distribution of individuals in litter treatments. Those species listed as immatures were identified to morphospecies.

SPECIES	Flat Filter Paper Disks	Curled Filter Paper Disks	Flat Maple Leaves	Curled Maple Leaves
Family Theridiidae				
<i>Enoplognatha ovata</i> (Clerck) (= <i>Theridion redimitum</i> [L.])	14	37	56	114
Family Linyphiidae				
<i>Bathypantes pallida</i> (Banks)	1	4	13	2
sp. 1 (immature)	3	7	1	3
sp. 2 (immature)	1	1	0	7
Family Agelenidae				
<i>Circurina brevis</i> (Emerton)	2	6	3	6
<i>C. robusta</i> Simon	2	2	3	7
<i>C. sp. 1</i> (immature)	1	0	3	1
<i>C. sp. 2</i> (immature)	0	0	0	1
Family Hahnidae				
<i>Neoantisetia agilis</i> (Kerserling)	1	2	0	2
<i>N. sp. 1</i> (immature)	0	1	0	1
Family Lycosidae				
<i>Pirata sp. 1</i> (immature)	0	0	0	1
Family Anyphaenidae				
<i>Anyphaena sp. 1</i> (immature)	0	4	0	5
Family Salticidae				
sp. 1 (immature)	1	0	1	1
TOTAL	26	64	79	152

Litter boxes were used to measure the influence of leaf shape on litter spider community structure since they permitted modification of leaf shape prior to placement in the field (Stevenson and Dindal 1981). Litter boxes (10 cm x 10 cm x 2 cm) were constructed of metal hardware cloth (6.35 mm openings). Large wandering spiders, such as lycosids, may be excluded from the litter boxes because of the small openings. This possibility is unlikely, however, since no adult lycosids have been collected in pitfall traps at this study site (Stevenson, unpublished data; Tardiff and Dindal, unpublished). The largest wandering spider collected in pitfalls was *Circurina robusta* Simon which was also collected in litter boxes.

Freshly-fallen sugar maple leaves were collected in October 1978. Leaves were wetted to saturation in distilled water and pressed flat in a plant press. Dried and flattened leaves were selected and separated into 60 batches of 10 leaves each. Similarly, 600 filter paper disks (9.0 cm in diameter, Whatman Company) were also separated into 60 batches of 10 disks each. Filter paper disks were chosen as a simulated leaf type to provide a non-nutritive substrate, of which the major variable would be leaf shape. Filter paper degrades primarily by weathering, not by biological decomposition processes, due to a high carbon: nitrogen ratio (Dindal and Levitan 1977).

Each filter paper disk and dried maple leaf was measured (± 0.01 cm²) on a LiCor Model 3100 Area Meter (Lamba Instrument Corporation, Lincoln, Nebraska). Surface area per leaf or disk was determined as the mean of four measurements. Average leaf or

Table 2.—Coefficients of correlation between spider species richness (number of species) and two habitat structure variables.

Litter Treatment	Variable	November-March (13 df)	April-August (13 df)
Curled Maple Leaves	Mean Leaf Size (B.E.) ¹	-.082	.001
	Mean Leaf Size (A.E.) ²	-.052	-.009
	Mean Tube Opening Size	.068	-.045
	Number of Spider Webs	.740**	.417
Flat Maple Leaves	Mean Leaf Size (B.E.)	.025	.134
	Mean Leaf Size (A.E.)	-.131	.402
	Mean Tube Opening Size	n.a. ³	n.a.
	Number of Spider Webs	n.a.	n.a.
Curled Filter Paper Disks	Mean Disks Size (B.E.)	-.325	.174
	Mean Disk Size (A.E.)	.009	.309
	Mean Tube Opening Size	-.394	.687**
	Number of Spider Webs	.191	.307
Flat Filter Paper Disks	Mean Disk Size (B.E.)	.232	-.073
	Mean Disk Size (A.E.)	.454	.288
	Mean Tube Opening Size	n.a.	n.a.
	Number of Spider Webs	n.a.	n.a.

¹ B.E. = before spider extraction.

² A.E. = after spider extraction.

³ n.a. = correlation analysis not appropriate.

**p < .01.

disk size per batch was calculated from the mean values recorded for 10 individual leaves or disks in each batch.

Curled leaves and disks were made by wetting each disk or leaf in distilled water until pliable and then rolling it by hand to form a tube. Each batch was allowed to dry and then it was placed in a litter box.

Although habitat space was not measured directly, curled litter provided more interstitial space than flat litter, on a qualitative basis, since flat litter formed tight layers and had a more compact appearance than curled litter. This compaction was especially evident in flat filter paper disks since they lacked microrelief, such as venation, which provided interstitial spaces.

A 10 m x 12 m grid with 1 m intervals was formed at the study site. Each litter box was randomly assigned to a position at the intersection of the grid intervals. All boxes were placed in the field by October 1, 1979; subsequent natural litter fall covered the boxes and was left in place. It partly helped to prevent rain damage to enclosed leaves or disks. Litter covering the boxes did not enter them and thus did not contribute to the litter treatments or influence litter structure.

Twelve boxes, three of each litter treatment type, were randomly selected for removal in each month from November 1979 to August 1980 and were individually sealed in plastic bags to prevent loss of arthropods. A similarly-sized sample of natural litter was also removed from the area adjacent to each box and sealed in a plastic bag. A previous study (Stevenson and Dindal 1981) revealed that the sample size was adequate to detect differences in arthropod communities between litter treatments. Spiders in litter boxes

Table 3.—Coefficients of correlation between *Enoplognatha ovata* density and three environmental variables.

Litter Treatment	Variable	November-March (13 df)	April-August (13 df)
Curled Maple Leaves	Mean Leaf Size (B.E.) ¹	-.288	.018
	Mean Leaf Size (A.E.) ²	-.155	.058
	Mean Tube Opening Size	-.006	.463
Flat Maple Leaves	Mean Leaf Size (B.E.)	.375	.099
	Mean Leaf Size (A.E.)	.225	.310
	Mean Tube Opening Size	n.a. ³	n.a.
Curled Filter Paper Disks	Mean Disk Size (B.E.)	-.234	.174
	Mean Disk Size (A.E.)	.011	.334
	Mean Tube Opening Size	-.394	.687**
Flat Filter Paper Disks	Mean Disk Size (B.E.)	.245	-.050
	Mean Disk Size (A.E.)	.630*	.083
	Mean Tube Opening Size	n.a.	n.a.

¹ B.E. = before spider extraction.

² A.E. = after spider extraction.

³ n.a. = correlation analysis not appropriate.

*p < .05.

**p < .01.

and natural litter samples were extracted in large, steep-sided Tullgren funnels and fixed in a solution of isopropyl alcohol:glycerin:water (80:10:10). Contents of all boxes and litter samples also were hand-sorted for additional spiders. Cephalothorax widths of all *E. ovata* individuals extracted from litter boxes and natural litter samples were measured with a micrometer. These data were extrapolated to the nearest 0.1 mm.

Following extraction, diameters of the two openings on each curled leaf or disk tube were measured to the nearest 1.0 mm. The presence of spider webs within the tubs was scored (present or absent). Leaves or disks from each litter box were wetted and pressed flat in the plant press following hand-sorting for spiders. After drying, each disk or leaf was measured with the area meter as described previously.

Three-way analyses-of-variance (ANOVA) were performed with leaf type (maple leaves or filter paper disks), leaf shape (curled or flat), and months (November through August) as independent variables. Dependent variables were spider species richness, equitability (J' ; Pielou 1966), and density of *E. ovata*. The relationships between two habitat structure indices (leaf or disk size and mean opening size of curled leaf or disk tubes) and species richness or *E. ovata* density was tested by product-moment correlation. Finally, differences in relative composition of spiders (guild composition and taxonomic families) were examined by tests of independence for R x C contingency tables (G-test; Sokal and Rohlf 1969).

RESULTS AND DISCUSSION

COMMUNITY ORGANIZATION

A total of 321 spiders were collected from litter boxes, representing 7 families and 13 species or morphospecies. A list of these species and the distribution of individuals is

given in Table 1. Those species listed as immatures were identified to the morphospecies level (see Stratton et al. 1979) since species-specific taxonomic characteristics (e.g., genitalia) either were not present on those organisms or could not be determined.

Species Richness.—Spider species richness (number of species) in litter boxes was analyzed to evaluate the importance of leaf shape to community organization of litter spiders. Litter boxes containing curled litter had more spider species than did boxes with flat litter (ANOVA $F_{1,80} = 7.198$, $p < 0.01$). Thus, the field experiment confirms the hypothesis that more spider species occur in curled litter.

The amount of habitat space in litter of different shape influenced patterns of spider species richness. Since flat leaves and filter paper disks formed tight layers with reduced interstitial space, fewer species could co-exist in such microhabitats than in curled litter which provided more habitat space. These results agree with positive correlations between forest litter habitat space and wandering spider species richness (Uetz 1975, 1979).

Correlations between species richness and habitat structure indices were calculated separately for each leaf treatment. They were also conducted for the first and second halves of the 10-month study period, since there are important seasonal differences in spider growth and metabolic activity (Moulder and Reichle 1972). All correlation coefficients were tested for statistically significant differences from zero by t-tests (Sokal and Rohlf 1969).

Within boxes of maple leaves (both curled and flat), number of spider species was not significantly correlated with any of the variables measured (Table 2). Within boxes of

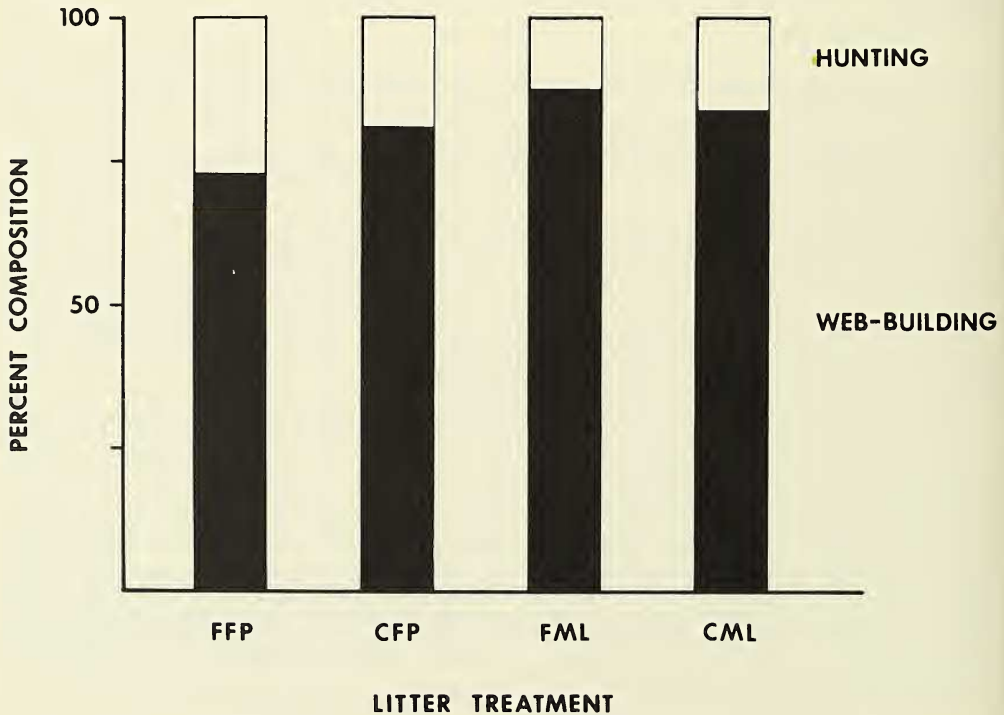


Fig. 1.—Composition of hunting and web building spider in litter boxes of four litter treatments. Hunting and web building species represent the two major foraging strategies of spiders. (Litter treatments: FFP = flat filter paper disks, CFP = curled filter paper disks, FML = flat maple leaves, CML = curled maple leaves).

curled filter paper disks, spider species richness was correlated ($p < 0.01$) with mean opening size of the filter paper tubes during the second half of the study period. Field observations indicated, at this time, that the ends of some filter paper tubes had been closed by rainfall impact and many individual tubes were completely flattened. This correlation suggests that spider diversity was limited by habitat space. Rain damage to these tubes caused reduction in habitat space which few species could exploit (see also Uetz 1975, 1976). Tubes of curled maple leaves retained their shape and thus access to tube interiors was unhindered.

Finally, spider species richness in litter boxes containing flat filter paper disks was correlated ($p < 0.05$) with mean size of filter paper disks following arthropod extraction. This occurred during the first half of the experiment (Table 2). This correlation is spurious since the size of filter paper disks exhibited extremely low variability. The coefficient of variation ($CV = \text{standard deviation}/\text{mean} \times 100$; Sokal and Rohlf 1969) of disk size for flat disks was 0.075 ± 0.004 ($\bar{x} \pm \text{S.E.}$; $n = 30$) before placement in the field and 0.688 ± 0.337 after extraction of spiders. Moreover, all other correlations between leaf or disk size and number of spider species were not statistically significant. Thus, leaf size does not appear to be an important factor influencing forest litter spider community organization. Similarly, Reice (1980) noted that arthropods in litter habitats react more to interstitial space than to substrate area.

Equitability.—Leaf shape had no effect on the equitability of spiders within species (ANOVA $F_{1,80} = 2.956$, $0.05 < p < 0.10$). This result contrasts with data from Uetz (1975) who found that equitability of wandering spiders was correlated with both depth

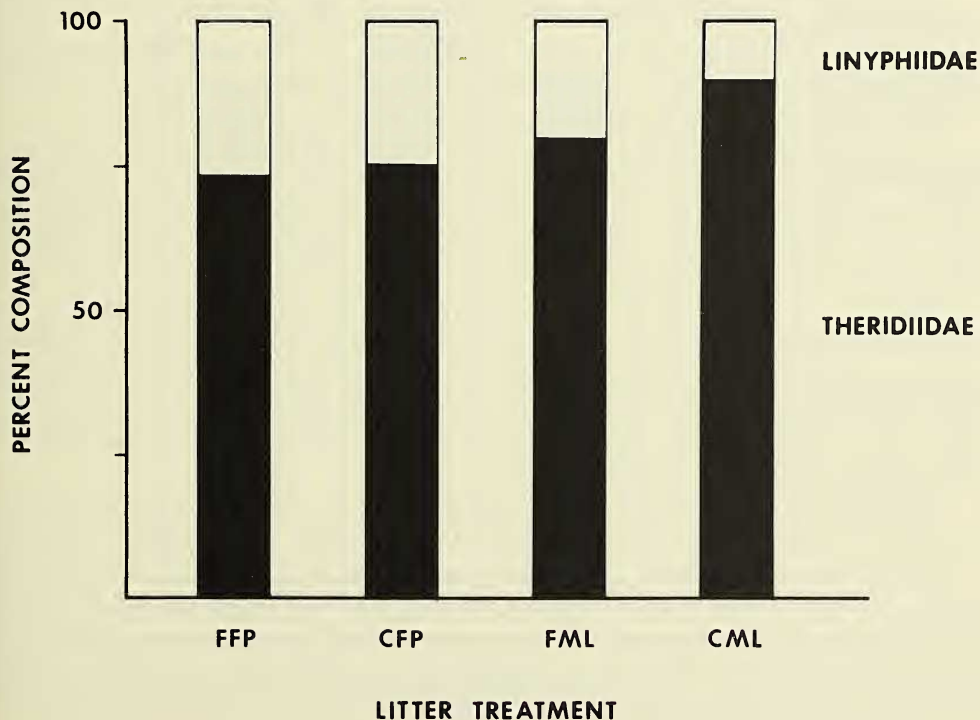


Fig. 2.—Composition of web building spiders by family in each of the four litter treatments. Litter treatment key given in Figure 1.

Table 4.—Monthly differences in mean density of *Enoplognatha ovata* in litter boxes. Differences in means were analyzed by Duncan's Multiple Range Test. Those means not connected by the same underline are significantly different at the .05 level.

Jul. 0.08	Aug. 0.08	Jun. 0.17	May 1.08	Feb. 1.67	Apr. 1.91	Nov. 2.50	Jan. 2.92	Apr. 2.92	Dec. 4.08
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and habitat space within forest litter. Uetz suggested that complex litter environments, which contain curled leaves, regulate spider species diversity by reducing differences in the relative abundance of species, in addition to increasing the number of species. Our results indicate that regulation of spider equitability in complex litter is not solely due to differences in leaf shape. Instead, increased survivorship of immature spiders in deep and complex litter, due to greater abundance of refuges from predation and cannibalism (Uetz 1975), may be the proximate cause of greater evenness in such habitats.

Guild Composition.—Composition of spiders in the four litter treatment types was compared according to method of prey capture: hunting spiders or web-building spiders. Hunting spiders included wandering species (after Uetz 1975) and jumping species. Within the web-building group, only Linyphiidae and Theridiidae were collected. Only species of the genus *Circurina* (hunting spiders) were found in the Agelenidae.

Similar percent compositions of spider functional groups were found in each litter treatment (Figure 1). Web-building spiders comprised 87.5%, 84.1%, 73.1%, and 76.6% of total spiders in flat maple leaves, curled maple leaves, flat filter paper disks, and curled filter paper disks, respectively. Percent composition of the two functional groups was not significantly different between litter treatments ($G = 4.652$, $0.1 < p < 0.5$).

Distribution of web-building spider families was also similar in the four litter treatments (Figure 2). Theridiid spiders comprised 80.0%, 89.8%, 73.7%, and 75.5% of web-building spiders in litter boxes of flat maple leaves, curled maple leaves, flat filter paper disks, and curled filter paper disks, respectively. Litter treatment did not affect relative composition of web-building spider families ($G = 3.934$, $0.1 < p < 0.5$).

Stratton et al. (1979) found similar proportions of hunting and web-building spiders on three coniferous tree species and suggested that there were similar basic resources (prey and spatial parameters) on all three trees. Since all litter boxes were located at the same study site, the four litter treatments supported similar prey types for spiders (Stevenson 1980). However, spatial properties of the four microhabitats differed considerably because of differences in leaf shape.

Differences in these spatial properties apparently caused important differences in composition of hunting spider families (Figure 3). For example, Anyphaenidae were found exclusively in boxes of curled litter (20% of total hunting spiders in boxes of both curled maple leaves and curled filter paper disks). Salticids were more prominent in boxes of flat litter (10.0% of hunting spiders in flat maple leaves, 14.3% in flat filter paper disks) than in boxes of curled litter (4.0% of hunting spiders in curled maple leaves, 0.0% in curled filter paper disks). Litter treatment had a significant influence on the relative composition of hunting spider families ($G = 15.612$, $p < 0.005$).

Although relatively little is known about the ecology of litter-inhabiting anyphaenids, they are similar to clubionids in morphology and habit (Kaston 1948, 1978). Clubionids

make tubular retreats in rolled-up litter leaves (Kaston 1948, 1978). Anyphaenids make similar retreats in the laboratory (Uetz pers. comm.) and may also build them in curled litter.

Salticid spiders occurred more frequently in flat litter than in curled litter (Figure 3). These jumping spiders orient to their prey visually (Kaston 1948) and need a solid platform from which to jump (Stratton et al. 1979). Flat maple leaves and filter paper disks provide greater unobstructed surface area as a jumping platform than does curled litter. Further, visual orientation to prey is enhanced in flat litter.

MICROHABITAT SELECTION OF IMMATURE *ENOPLIGNATHA OVATA*

A total of 289 individual *E. ovata* were collected from litter boxes and natural litter samples. All spiders were sexually immature. Further, this species was the dominant spider in all litter treatments (see Table 1).

Influence of Leaf Shape on Microhabitat Selection.—Relative abundance of *E. ovata* within litter boxes reflected microhabitat selection by this species. More spiders were found in curled litter than in flat litter (ANOVA, $F_{1,80} = 18.571, p < 0.001$). These data are consistent with published reports on the use of curled leaves by *E. ovata*. This spider is one of several web-building species which inhabit curled leaflets on *Mahonia aquifolium* (Waldorf 1976). Egg sacs of *E. ovata* are usually attached to the underside of a curled leaf (Kaston 1948).

Thus, there is considerable evidence that curled leaves are preferred microhabitats for *E. ovata*. Two hypotheses are suggested for preference of curled leaf microhabitats by this

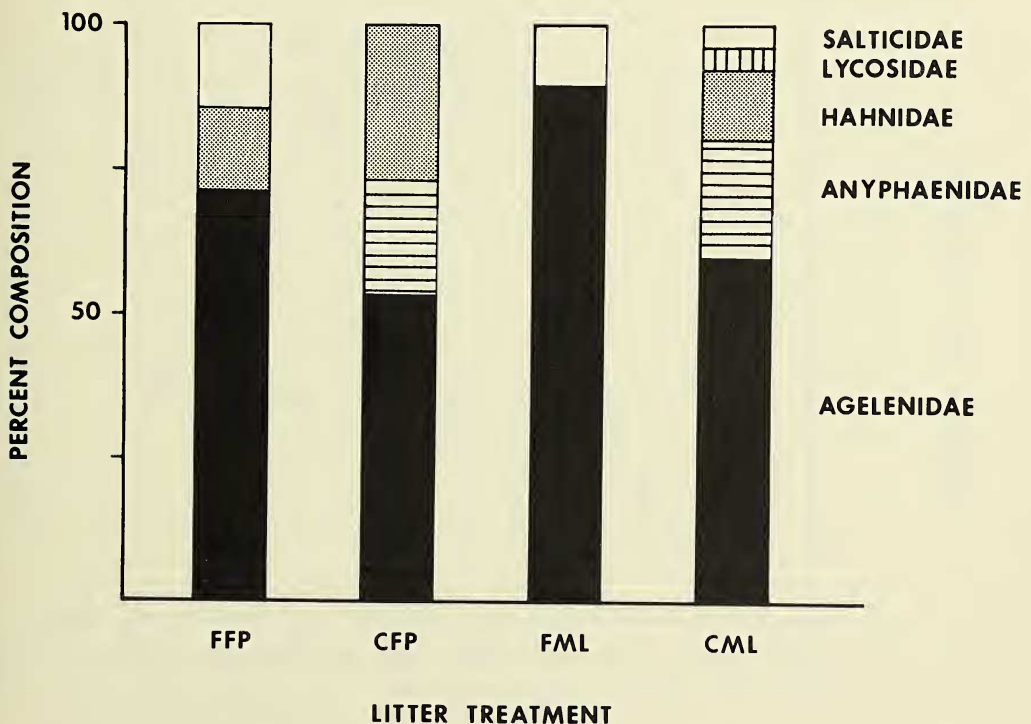


Fig. 3.—Composition of hunting spiders by family in each of the four litter treatments. Litter treatment key given in Figure 1.

species: (1) curled litter provides refuges from predation and hence contribute to increased survivorship of individuals inhabiting them, and (2) curled litter provides suitable web sites due to architectural properties of the microhabitat and large amounts of habitat space (see Uetz 1974, 1975). Previous studies suggest or demonstrate that litter complexity, including the presence of curled leaves, can reduce inter- and intra-specific predation among litter spiders (Edgar 1969, Hallander 1970, Uetz 1976, 1979). Further, the availability of web substrate, coupled with sufficient habitat space for web construction and function, are among the most important environmental factors limiting distributions of web-building spiders (Lowrie 1948, Turnbull 1960, Duffey 1966, Enders 1973, 1974, Robinson 1981). Habitat space within forest litter increases as the percent of curled leaves increases (Uetz 1974, 1975, Bell and Sipp 1975). Our data are insufficient to completely discriminate between these two hypotheses for explanation of microhabitat selection by *E. ovata*. However, during the first half of the study period, *E. ovata* density was correlated ($p < 0.01$) with the number of spider webs in tubes of curled maple leaves (Table 3). This correlation suggests that most of the spiders which inhabited these microhabitats built and used webs. Spatial properties of the leaf tubes no doubt were important for web construction.

Maple leaves supported greater density of *E. ovata* than did boxes with filter paper disks (ANOVA, $F_{1,80} = 31.101$, $p < 0.001$). Differences in amounts of habitat space, according to leaf type, explain these results. Since maple leaves have surface microrelief (e.g. venation), adjoining leaves in the flat maple leaf treatment retain interstitial space, whereas flat filter paper disks compact completely. Thus, more spiders are able to occupy the greater habitat space in flat maple leaves.

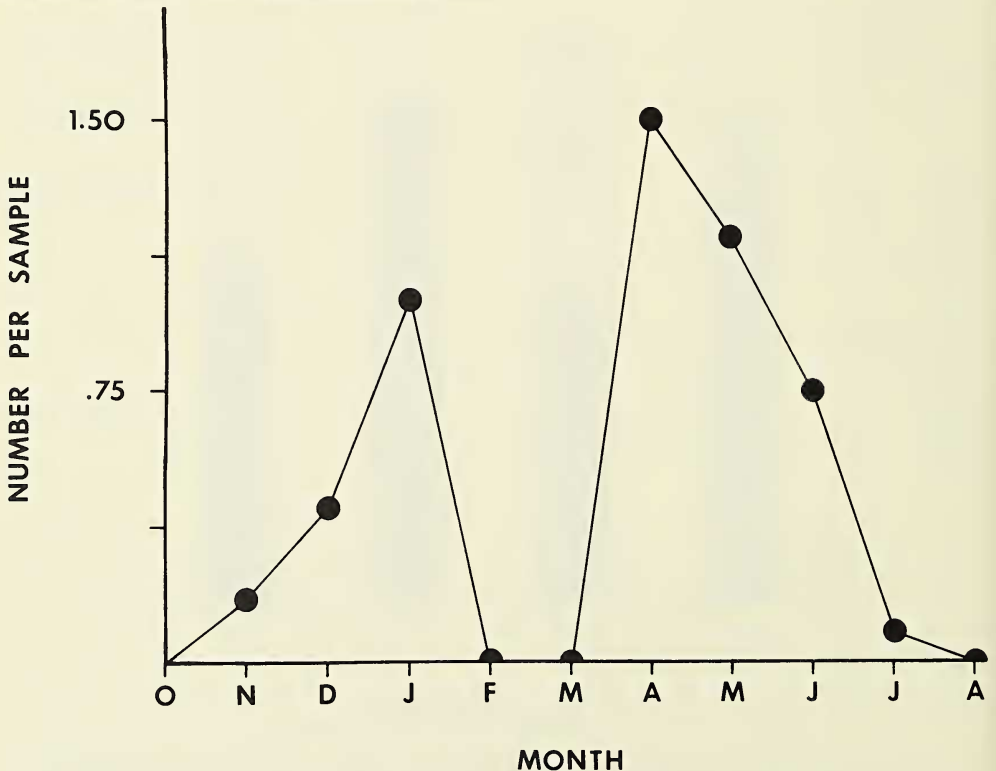


Fig. 4.—Monthly variation in density of *Enoplognatha ovata* in natural litter samples (\bar{x} ; $n = 12$).

Spider density was correlated ($p < 0.01$) with mean open tubular diameter of curled filter paper disks during the second half of the experiment (Table 3). At this time, some curled filter paper tubes and their openings were compacted by rainfall which caused reductions in habitat space. Density of *E. ovata* was limited by this reduced habitat space. Curled maple leaves retained their shape and habitat space throughout the experiment. Hence, *E. ovata* was not prevented from colonizing curled maple leaves.

Forest litter habitat space is a function of leaf size as well as leaf shape and litter depth. Greater interstitial space occurs between large leaves than between small ones. Thus, microhabitat selection of *E. ovata* may be related to leaf size. However, correlations between *E. ovata* density and mean disk or leaf size were not significant (Table 3). Thus, leaf size does not appear to influence its microhabitat selection.

Influence of Life History on Microhabitat Selection.—There were significant seasonal differences in *E. ovata* abundance (ANOVA, $F_{9,80} = 7.190$, $p < 0.001$). Months in which there were population density maxima in litter boxes (November through January and April) were different ($p < 0.05$) from all other periods (Table 4). A significant interaction occurred between leaf type and month (ANOVA, $F_{9,80} = 2.802$, $p < 0.01$), which indicates that *E. ovata* density was more variable in maple leaves than it was in filter paper disks. Further, *E. ovata* density in natural litter was highest in January and in April to May (Figure 4). These months correspond to the times density maxima occurred in litter boxes. Thus, these monthly differences in *E. ovata* density reflect differential microhabitat selection by season.

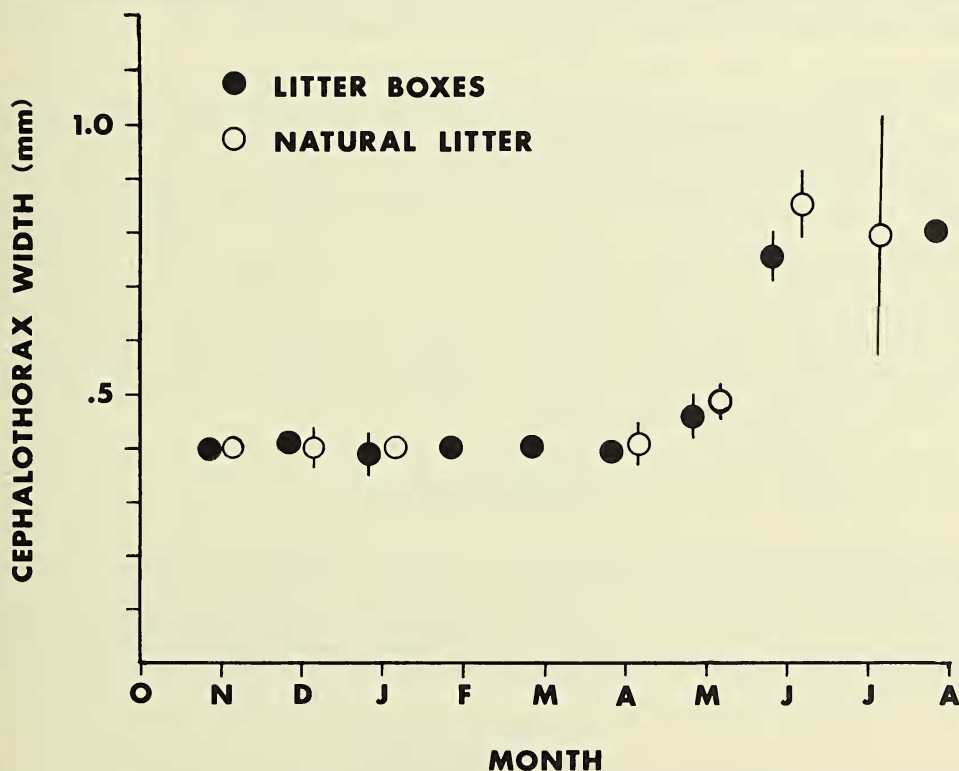


Fig. 5.—Monthly variation in cephalothorax width of *Enoplognatha ovata* in litter boxes and natural litter samples ($\bar{x} \pm SE$; $n = 12$).

Two other pieces of evidence reveal that changes in ontogeny of this species influence its microhabitat selection. First, cephalothorax widths from spiders extracted from litter boxes were compared to cephalothorax widths from spiders from natural litter (Figure 5). Body size of these spiders remained essentially constant in both natural litter and litter boxes from November through April. From May to August, spider body size increased, although spiders were absent from litter boxes in July and from natural litter in August. Thus, growth of this spider occurred in the second half of the experiment, particularly from May to June.

Second, during summer months (particularly June and July), many large, sexually mature *E. ovata* spiders were found on webs attached to the undersides of understory tree leaves. Waldorf (1976) found that *E. ovata* inhabited leaflet microhabitats on *Mahonia aquifolium*, a forest understory plant. Mature specimens of this spider species are found on bushes and trees in July, when mating occurs (Kaston 1948). Thus, growing spiders disperse from forest litter in summer and occupy microhabitats on leaves in the forest understory.

These results are consistent with previously-documented evidence for spider growth and dispersal. Growth of forest litter spiders is often quite rapid in spring and early summer (Moulder and Reichle 1972). Associated with increased spider body size are increased needs for energy (food intake) and space (e.g., for larger webs). Dabrowska-Prot and Luczak (1968) and Enders (1974) demonstrate that, as web-building spiders mature and grow in size, they often choose web sites at greater heights above the ground than smaller conspecifics. This is also considerable evidence that larger spiders with webs well above the ground feed on larger prey (Enders 1974, Waldorf 1976).

CONCLUSION

Leaf shape is one variable in a complex association of variables which together constitute the forest litter habitat. Other such variables are litter depth and microclimate, which are easily measured, and number of microhabitats and spatial arrangements of litter units, which are less easily quantified. These latter variables may differ for individual species depending on spider size and spatial requirements. Leaf shape is shown to influence directly the number of species within forest litter and microhabitat selection of some species (e.g., *E. ovata*) and higher taxa (e.g., Anyphaenidae). Future research should attempt to clarify whether distribution patterns of individual species are due to architectural properties of the substrate, to interspecific interactions such as predation, or to combinations of these and other factors.

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